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A MOUNTED SKELETON OF THE GIANT PLESIOSAUR *KRONOSAURUS*

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In 1924 Longman described a plesiosaur mandibular fragment of large size from the Lower Cretaceous of Queensland as the type of a new genus and species, *Kronosaurus queenslandicus*. Later (Longman 1932), some further fragmentary material, mainly the proximal ends of two limb bones, was obtained from the type locality near Hughenden, and a letter from Dr. Longman to Mr. W. E. Schevill in November 1932 mentions the discovery there of eight caudal vertebrae which appear not to have been described. The limb bone material, added to the evidence of the jaw fragment, indicated a plesiosaur of very large size. The remains suggested relationship to *Peloneustes*, and Longman (1932) published a hypothetical restoration of *Kronosaurus* based mainly on the work of Andrews (1913, fig. 26) on *Peloneustes philarchus*.

In 1931-32, Mr. William E. Schevill, a member of an expedition sent to Australia by this museum, explored the Queensland Lower Cretaceous deposits in the Richmond region, west of Hughenden. In Grampian Valley, 30 miles to the north of Richmond, he found a rostrum of a young individual of *Kronosaurus* (MCZ No. 1284). His attention was called, by a local resident, to the Army Downs region, five miles farther north. Here was found the skeleton (MCZ No. 1285) which is described below.

The specimen had been entombed, in an articulated state, dorsal surface up, in a limestone matrix. In recent times, however, the skeleton had been subject to erosion, so that it consisted

essentially of a series of limestone nodules, freed from the underlying strata and nearly completely buried in the soil. Skull, neck, trunk and part of the tail were contained in a linear series of 15 nodules of varied size. Of these the first had been displaced and overturned; the others, however, appear to have undergone little or no displacement. Erosion had destroyed much of the outer parts of the nodules, so that, for example, most of the superficial bones of the skull had been destroyed, part or all of many of the neural spines had vanished, and the girdles, ribs and abdominal armor are incomplete. Erosion had, further, destroyed some of the contacts between successive blocks, but because of their seemingly undisturbed position, interpolation of materials once filling the gaps can be made with considerable confidence. No trace of the pectoral limbs was preserved. The pelvic limbs were present in normal articulation, extending out on either side from the large block containing the pelvic region, but even the femora were badly weathered and the more distal regions of the "flippers" were very poorly preserved.

The blocks, weighing in all nearly four tons, were excavated and shipped to Cambridge by Mr. Schevill. Two years later the skull was developed by Dr. T. E. White, and a description published by him (1935). Because of the very considerable outlay of time, energy — and money — necessary for the laborious task of preparation, the postcranial material lay untouched in storage for two decades. Three years ago, however, Mr. Godfrey Cabot, who is deeply interested in the subject of marine reptiles, furnished us with funds sufficient to pay the costs of preparing and mounting the skeleton. The work was directed by the junior author, with the assistance of Messrs. James A. Jensen and David Fuller.

As noted above, erosion had destroyed a fair fraction of this once complete and articulated skeleton, so that approximately a third of the specimen as exhibited is plaster restoration. There are, nevertheless, few points in which any great deviation from verity can have occurred in mounting the skeleton. As noted below, the exact number of cervical plus trunk vertebrae is uncertain, as is the length of the short tail. Trunk rib lengths are for the most part uncertain, but the curvature of the ribs as preserved furnished a rather safe guide to trunk proportions.

The front paddles are lacking, but can be restored with considerable confidence by comparison with preserved parts of the pelvic appendages. Upon completion of the mount, the only structural feature which we would wish to modify, given the opportunity, would be to move the pelvic girdle upward and backward by perhaps 20 cm.

Longman, we have noted, compared *Kronosaurus*, on the basis of the fragmentary remains available to him, to *Peloneustes* of the Oxford Clay. Our skeleton confirms his belief in the main. As will be seen from the description below, we are dealing with a pliosaur of somewhat similar nature, although of much larger size — our animal has about four times the linear dimensions of Andrews' restored skeleton with a total length, as restored, of 1280 cm. — about 42 feet. The head, however, is relatively larger in *Kronosaurus*, making up slightly over one-fourth of the total length, whereas in *Peloneustes* the skull is but one-fifth the length of the animal. Further, the trunk is relatively long in the Australian giant, and the neck extremely short; although the number of presacral vertebrae in *Kronosaurus* and *Peloneustes* is approximately the same, the beginning of the dorsal rib series and the position of the shoulder appears to have been about 10 vertebrae farther forward in our specimen. *Kronosaurus* thus appears to be the most stoutly built of plesiosaurs.

As a short-necked pliosaur, it is of course exceeded in length by some of the long-necked elasmosauroid types. In bulk, however, it seems certainly to be larger than any described plesiosaur, although Dr. L. B. Tarlo (*in litteris*) tells us that material of a Kimmeridge Clay pliosaur indicates an animal of comparable size.

As far as preserved, the *Kronosaurus* postcranial skeleton does not depart structurally in any marked manner from the general pliosaurid pattern, and hence need not be figured or described in detail. The notes given here can be followed by reference to the excellent descriptions and figures given by Andrews (1913) for Oxford Clay pliosaurs.

Vertebral column. The series of nodules containing the skeleton yielded part or all of 46 vertebrae between the atlas-axis and the proximal part of the tail. The sequence of the preserved vertebrae can be determined in every case from the sequence of

the blocks containing them. But while various short series are in articulated position within a given block, and certain of the blocks were in contact, there are obvious gaps in the series, and we have restored 11 vertebrae in filling out the column to the proximal part of the tail. For the most part the number of missing vertebrae in these gaps can be determined with considerable confidence, through the relation of adjacent vertebrae to other structures, or the length of the eroded interval between blocks. It is possible that our restored vertebral count may vary by one or two segments from the true condition.

Anteriorly, vertebrae 1-5 were found in position behind the skull. Following a short gap, 4 further vertebrae were present in another block. The first of this succeeding series is nearly complete; the third has a complete rib (on the right side). From the evidence of rib lengths, position of rib facets, centrum dimensions, and the length of the gap between blocks, interpolation of 3 vertebrae between the first and second series appears reasonable, and we shall consider the second series to include vertebrae 9 to 12. An isolated neural spine and arch appears from its proportions and the nature of the rib facet to have occupied a short gap following vertebra 12. The next block contained vertebrae 14-16. It was necessary to break up, in the field, the large mass containing the pectoral girdle region: This caused two further gaps, the first of which can be accurately determined to involve one segment; the second, following a series of 5 vertebrae — presumably 18-22 — seems certainly to have been occupied by 3 vertebrae. There follows a series of 4 vertebrae, our numbers 26-29. Behind this is a block with 2 vertebrae separated by gaps both fore and aft. The first gap is of a length appropriate for 2 vertebrae; the second gap is short, but because of the imperfect nature of the vertebra behind it, it is uncertain whether a segment should be intercalated here, as we have done in the mount. Back of this point, an unbroken series of vertebrae, which we have restored as numbers 35-43, can be traced to a point close to the puboischial suture on the underlying pelvic girdle. Here 1 vertebra is definitely missing, followed by vertebrae 45-48, found above the ischium, and 49-50 close behind them. Three further adjacent blocks contain 4 vertebrae and parts of the centra of 3 others, bringing the total as restored to this point to 57 vertebrae.

From the rapid decrease in size seen within the post-pelvic series, it is obvious that the tail was short; we have restored it to give a total number of 79 vertebrae. As will be seen from the description of the rib attachments given below, there appear to be 12 true cervical vertebrae, 2 "pectorals," probably 30 dorsals, giving a total of approximately 44 presacra, followed by 3 or 4 sacra.

Centra. Measurements (in mm.) of some of the best preserved centra are as follows:

<i>Centrum</i>	<i>Length</i>	<i>Width</i>	<i>Height</i>
4	102	181	193
9	93	180	210
15	114	182	233
20	123	202	225
27	145	213	217
35	143	205	208
42	136	182	201
50	118	180	198
54	108	157	172

As can be seen, the length and width of the centra reach a maximum in the mid-dorsal region, with somewhat decreasing measurements toward the sacrum, and a sharp drop in size — particularly in length — in the proximal part of the tail. The height of the centrum is much more uniform, with a fairly marked increase along the neck to the anterior dorsals, and a very gradual reduction back of this point to the proximal caudals. In consequence of the differences in width-height relations, the proportions of the vertebrae, as seen in end view, differ considerably from one region of the column to another. Mid-dorsals and posterior dorsals are nearly circular in outline; anterior dorsals are considerably taller than broad, giving an oval contour, and both the cervicals and the posterior vertebrae, from the posterior dorsals back, are moderately taller than broad. The cervicals and anterior dorsals are about twice as high as long; however, the length of the centrum increases posteriorly along the dorsal series, while the height decreases, so that towards the sacral region the height is but half again the length; in the tail, with

reduction taking place more rapidly in length than in height, there is some increase posteriorly in relative height.

Typical dorsal centra have the simple outlines of a short spool, with a smoothly curved lateral surface between raised anterior and posterior rims. Anteriorly and posteriorly, however, the presence of rib attachments modifies the lateral surfaces, as noted in more detail in the next section. In the cervicals the rib facets take the form of a circular "crater," with raised rims, occupying nearly the whole length of the lateral surface of the centrum. In the caudal region the low rib facet is of smaller dimensions. Above, it is joined by a vertical ridge, half way between anterior and posterior margins, which ran upward to the neuro-central suture. Below the rib facet, the preserved caudals, except the first two, are excavated laterally below a curved longitudinal ridge which is convex ventrally.

No chevrons were found with the few caudals present; however, presumed caudal 4 is bevelled ventrally on either side for chevron attachment.

Neural arches and spines. The axis neural spine is of large size. Many of the cervical spines behind this point are preserved. They are slender at the base, well tilted back and, in at least the posterior cervicals, broadened distally with a pronounced median groove, presumably for the attachment of ligaments. The anterior margin has a well-developed median keel for most of its height. Many of the dorsal spines are incomplete or absent; however, their general nature is apparent. They are broader at the base, and less inclined backward than the cervicals; the anterior keel is less pronounced and the distal grooving is absent. Three proximal caudals have partially preserved spines which slant strongly toward the rear. In the cervical region there are well developed zygapophyses. In the anterior part of the dorsal region zygapophyses are present, but reduced in size. Many of the neural arches of the more posterior vertebrae are imperfectly preserved or are absent, but it is significant that no trace of zygapophyses has been seen on any vertebra posterior to No. 27 (including several seemingly complete posterior dorsal and proximal caudal arches). Apparently connections between neural arches were made here, in piscine fashion, by ligaments alone.

Rib articulations. On the atlas-axis, a small conical tubercle is present, low down on either side at about the level of the suture between atlas intercentrum and centrum; presumably this represents a small fused rib. With the axis centrum there begins a series of cervical rib facets, oval in shape, with raised borders. No clear distinction could be seen between presumed dorsal and ventral areas of attachment. In the most anterior vertebrae the facets are situated low down on the centrum, with their lower rims about 2.5 cm. above the bottom margin of the centrum. The anterior ones are short ovals in outline, with the longer axis vertical, and measuring about 7 by 8 cm. Anteroposteriorly these facets cover most of the lateral surface of the centrum. On the 9th and 10th vertebrae the facets have moved upward to some extent, so that their lower margins are about 3.5 cm. above the level of the bottom of the centra. Here the surface is more markedly oval in shape, with diameters of about 5.5 and 10 cm. At vertebra 12, the upward tendency is more pronounced; the dorsal margin of the facet is at the line of suture between arch and centrum, and the surface measures 6 by 10.8 cm. As noted above, centrum 13 is missing. However, vertebra 14 is of the transitional type which has been termed "pectoral" (this vertebra appears to have lain above the scapula). The articular rib facet measures 5.5 by 11 cm.; its upper third lies definitely on the neural arch. Further, there is the beginning of a "transverse process"; the lower part of the articular area extends outward about 3 cm. beyond the level of the surface of the centrum, and the upper, neural arch portion is similarly produced.

Presumably the "pectoral" shift began with vertebra 13; by vertebra 15, there is a developed transverse process. This extends directly laterally to a distance of 19 cm.; the upper margin of the articular surface, which measures 6.5 by 13 cm., is at the level of the zygapophysial facets. The centrum forms a considerable part of the root of the process, but whether it reaches the facet surface is uncertain. On vertebra 16 the centrum enters broadly into the formation of the root of the transverse process, but fails to reach its distal end. On vertebra 18 the centrum buttresses a small area of the base of the process, with a ventral keel extending out from this area along the underside of the process. By vertebra 19 this keel has disappeared, the lower surface of the

process is smoothly rounded, and the process springs from a point well above the arch pedicel. Here the dorsal surface of the process slants somewhat upward distally, extending out about 20.5 cm. from the midline. The processes in this region have become circular in section, measuring about 5 cm. in diameter at half-length, but somewhat expanded distally to an oval articular facet measuring about 7 by 11 cm. From this point back there is little change to be seen over much of the dorsal region in such processes as are well preserved. By vertebra 36, for example, the process, which here extends 19.5 cm. from the midline, has a diameter at midlength of about 6.5 cm., but expands distally to a nearly circular facet with a 7.5 cm. diameter. There is a slight posteroventral ridge development on the underside of the process, which is here directed somewhat posteriorly but does not rise appreciably toward its distal end. Similar processes are present to vertebra 43; but on this last vertebra the ventral ridge has increased in depth, so that the base of the process extends down to a point just above the suture between arch and centrum.

Vertebra 44 is missing. The following vertebra lacks the distal end of the process but its well preserved basal portion is narrow but tall, measuring 10.2 cm. in height, and although the line of suture is not clear, the lower two-fifths of the process definitely arises from the centrum. We are dealing with a sacral, and it is probable that vertebra 44 was a sacral as well. Vertebra 46 is also a sacral; the rib process is still deeper, measuring 11.8 cm. in height distally, and with a width not exceeding half the height. Approximately half the articular surface is furnished by the centrum. The process is much shorter than that of the dorsal vertebrae, extending only 13 cm. from the mid-line; further, its upper margin slants slightly downward and outward. The transverse process of 47 is smaller than that of 46, although similarly built, extending outward only 12 cm. and with a distal height of 8 cm. Possibly this was a further sacral. There is, however, no marked break between sacral and caudal elements.

Caudal rib facets can be followed for 7 vertebrae further. On vertebra 48 the lower margin of the base of the process has retreated upward a centimeter or more from the position found in 47; from this region backward, however, the ventral margin of the base moves ventrally so that by vertebra 55 it lies below

the middle of the lateral surface of the centrum. Even more marked is a downward movement of the upper margin of the rib facet. Beyond vertebra 50 the neural arch takes no part in rib support, the depth of the transverse process diminishes, and from vertebra 53 back its attachment is an essentially circular facet centrally placed on the lateral surface of the centrum. There also takes place a gradual reduction in length of the transverse process, so that by vertebra 54 it is little more than a circular area projecting but slightly from the general contours of the centrum.

Ribs. On the first five vertebrae the ribs are fused to the centra and, except for the loss of most of rib 5 on the right side, were nearly completely preserved. The first rib, as noted, is represented by a short spine fused, without evidence of suture, to the vertebra; on ribs 2-5 the line of suture is evident, although rib and centra were coössified. These anterior cervical ribs are short and stout. They extend outward and somewhat backward, flattened dorsoventrally. The distal ends are somewhat expanded, the expansion being directed backwardly from the line of the shaft. Rib 9 on the right side is nearly complete, with an estimated total length of 140 mm. The head is large, measuring 99 by 55 mm., with the greater diameter vertical; the rib extends at first directly outward, but then turns sharply backward, with a twist such that the dorsal margin of the head turns to the back margin of the shaft. Distally, the rib thins to an oval, with diameters of 57 and 30 mm. at 13 cm. from the head, the major axis running from posterodorsal to anteroventral margins. Rib 11 is similarly built.

The more posterior cervical and "pectoral" ribs are poorly preserved. One distal rib segment which appears to have lain in the pectoral region shows a much flattened shape, 86 by 35 mm. in section, with a terminus which is little expanded. Presumably this rib bore part of the serratus musculature, which one may expect to have been present—even if feebly developed—in plesiosaurs. Of the dorsal ribs, considerable material was preserved, but most had been disarticulated and badly broken. Those of vertebrae 22 and 23 alone are articulated and nearly complete. The heads are large, that of rib 23 having diameters of 102 by 88 mm. The total length of rib 23 was approximately

98 cm. The rib extends straight out from the transverse process for about 18 cm.; in the next 20 cm. there is a marked downward curvature to the extent of about 60° , followed by a further more gentle curvature to reach a total of 90° from the line of the transverse process and head. The shaft is somewhat flattened, with diameters, in section, of 58 and 47 mm. Distally the rib expands, terminating in an unfinished surface, for the ventral rib segment, which measures 80 by 65 mm.

Many of the fragments of more posterior ribs suggest similar proportions, except that the preserved heads of some of these ribs are more nearly circular in section. The sacral ribs are poorly preserved, and caudal ribs are absent in the material.

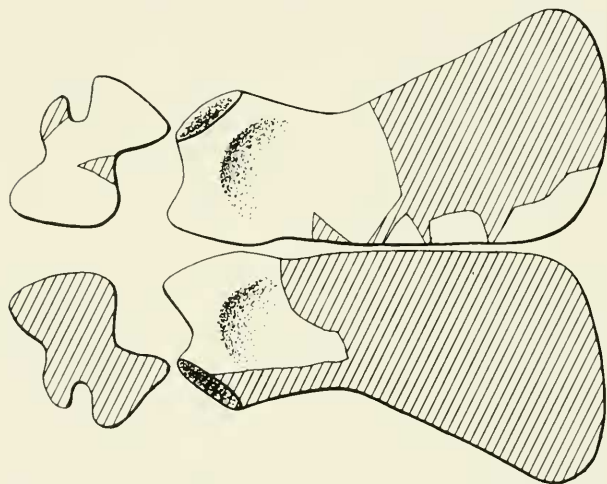


Fig. 1. Shoulder girdle of the mounted specimen in dorsal view. Hatched areas restored. X 1/30.

Girdles. White (1940, fig. 11a) has given a sketch of the shoulder girdle (Fig. 1). No remains of dermal elements were recovered. The right scapula, similar in shape to that of *Peloncostes*, is nearly complete, except for the dorsal blade; the left scapula was not found. Of the coracoids, much of the anterior half was present on both sides. Farther back, three portions of the medial margin of the right coracoid, shown in the

figure, were in place. From them the outlines of the coracoid can be fairly accurately restored, except for the degree of development at the posteroexternal angle. As restored, the coracoid is extremely long (160 cm.). This figure is 270 per cent of the width of the bone, measured from the outer margin of the glenoid process to the midline (59 cm.). In *Peloneustes philarchus* and *Simolestes*, as figured by Andrews (1913, figs. 8, 21), the coracoid length is about twice the width. The *Kronosaurus* coracoid is thus even longer proportionately than in typical pliosaurs.

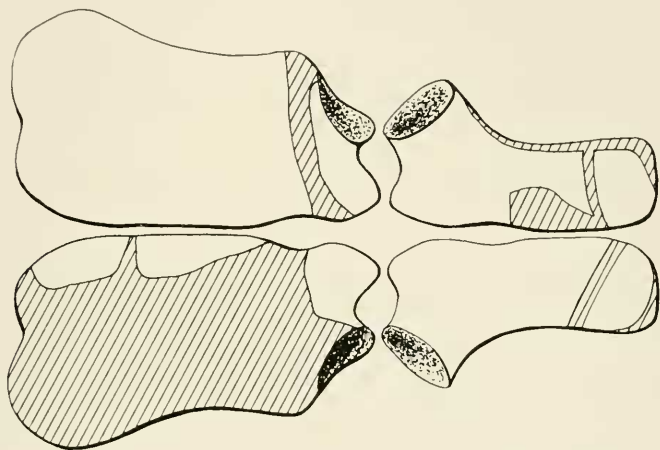


Fig. 2. Pubis and ischium of the mounted specimen in dorsal view. Hatched areas restored. X 1/30.

The pelvic girdle (Fig. 2) is exceptionally long. The left pubis is represented only by a small piece at the posterior end and two symphyseal fragments, but the right pubis is nearly complete. The element measures 128 cm. in length, with a greatest width posteriorly of 74 cm. This is, again, an elongate bone, with the width 173 per cent of the length, contrasted with 122 per cent, 118 per cent and 122 per cent in Andrews' figures of *Peloneustes*, *Simolestes* and *Pliosaurus* (Andrews 1913, figs. 24, 10, 7). Except for part of the external and posterior margins, the ischia are nearly complete. The greatest length is 103 cm., the width to the outer margin of the acetabulum 52 cm. The proportions of

the ischium (in contrast to the pubis) are not far from those of certain other pliosaurs, for the greatest length is 198 per cent of the width, as compared with figures of 189, 186, and 163 for the three pliosaurs mentioned above. In consequence, the bone is somewhat small in proportion to the pubis, for it is but 80 per cent of the length of the pubis in our skeleton whereas it is 118 per cent, 112 per cent, and 103 per cent in the three other pliosaurs described by Andrews. There is a well-defined but small puboischial vacuity. As in plesiosaurs generally, the pubes and ischia are considerably thickened medially below the acetabulum, indicating the presence of a very stout diamond-shaped symphyseal cartilage. Of the ilium, the basal portion, with a breadth of 17.7 cm. and a greatest height of 38 cm., is preserved. The contours of this portion indicate that the iliac blade was considerably expanded.

Limbs. As noted, no remains of the pectoral paddles were preserved. Both pelvic limbs had been in position, but were in great measure eroded. The femora were present, but the middle of the shaft was missing on both. However, the gap in the left femur was short; as the bone lay, this was less than 10 cm., and the bone has been restored to this extent, with a total length of 106 cm. The contacts between left femur and tibia and fibula are lost, but most of the tibia and the anterior part of the fibula are present. Articulated with them are the two elements sometimes termed intermedium and fibulare and, beyond, two large distal tarsals and metatarsals III and IV. A fragment from the right limb includes the more posterior of the two distal tarsals seen on the left, and attached to it distally, metatarsals III and IV in addition to a fragment of metatarsal V.

Described plesiosaurs in general have the forelimb and mesopodial elements arranged (to borrow a phrase from mammalian osteology) in an "alternating" fashion, so that (as in the carpus of advanced ungulate mammals) the elements in each row alternate to some degree with those proximal and distal to them, and facets between successive elements may be tilted at an angle from a transverse line of the bone. Here, on the contrary, there is, in the elements preserved, a one-to-one relation of bones of the three proximal rows, and the lines of articulation between successive segments are directly transverse. A similar construction

is present in a plesiosaur from the Kimmeridge Clay of Stretham now being described by Dr. Tarlo.

In both paddles a number of disarticulated and variably weathered phalanges, measuring on the order of 10 to 12 cm. in length, were present. The size of the limb elements present suggest a paddle, beyond the femur, of about twice the length of that of *Peloneustes philarchus*, i.e., about 120 cm. to 140 cm., and a total length of the limb of about 230 cm.

Hyoids. Beneath the cervical vertebrae was found a symmetrical pair of bones with expanded, diagonally-facing "heads"; neither is complete distally; the one with the longer shaft measures 262 mm. as preserved. These appear to be a pair of basihyoid elements; they differ markedly, however, from the slender elements generally reported in plesiosaurs.

Gastralia. A portion of the ventral armor was preserved, but the materials are too imperfect to warrant detailed description. There is evidence indicating that at least a part of the gastralia were of complex form, in contrast to the primitive rod-like shape.

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The skeleton of *Kronosaurus queenlandicus* as exhibited in the Museum of Comparative Zoology. Length as restored, 1280 cm.